

Memory



ISSN: 0965-8211 (Print) 1464-0686 (Online) Journal homepage: https://www.tandfonline.com/loi/pmem20

# Exploring the influence of encoding format on subsequent memory

Indira C. Turney, Nancy A. Dennis, David Maillet & M. Natasha Rajah

To cite this article: Indira C. Turney, Nancy A. Dennis, David Maillet & M. Natasha Rajah (2017) Exploring the influence of encoding format on subsequent memory, Memory, 25:5, 686-696, DOI: 10.1080/09658211.2016.1206942

To link to this article: https://doi.org/10.1080/09658211.2016.1206942



Published online: 25 Jul 2016.



🕼 Submit your article to this journal 🗗

Article views: 255



View related articles



View Crossmark data 🗹

# Exploring the influence of encoding format on subsequent memory

Indira C. Turney<sup>a</sup>, Nancy A. Dennis<sup>a</sup>, David Maillet<sup>b</sup> and M. Natasha Rajah<sup>c</sup>

<sup>a</sup>Department of Psychology, Pennsylvania State University, University Park, PA, USA; <sup>b</sup>Department of Psychology, Harvard University, Cambridge, MA, USA; <sup>c</sup>Department of Psychiatry, McGill University, Montreal, Canada

#### ABSTRACT

Distinctive encoding is greatly influenced by gist-based processes and has been shown to suffer when highly similar items are presented in close succession. Thus, elucidating the mechanisms underlying how presentation format affects gist processing is essential in determining the factors that influence these encoding processes. The current study utilised multivariate partial least squares (PLS) analysis to identify encoding networks directly associated with retrieval performance in a blocked and intermixed presentation condition. Subsequent memory analysis for successfully encoded items indicated no significant differences between reaction time and retrieval performance and presentation format. Despite no significant behavioural differences, behaviour PLS revealed differences in brain-behaviour correlations and mean condition activity in brain regions associated with gist-based vs. distinctive encoding. Specifically, the intermixed format encouraged more distinctive encoding, showing increased activation of regions associated with strategy use and visual processing (e.g., frontal and visual cortices, respectively). Alternatively, the blocked format exhibited increased gist-based processes, accompanied by increased activity in the right inferior frontal gyrus. Together, results suggest that the sequence that information is presented during encoding affects the degree to which distinctive encoding is engaged. These findings extend our understanding of the Fuzzy Trace Theory and the role of presentation format on encoding processes.

Distinctive encoding is necessary for subsequent successful memory of episodic events. To that end, Craik and colleagues (Jacoby, Craik, & Begg, 1979) proposed the distinctiveness of encoding hypothesis, which states that certain types of processing, including the depth of processing and the degree of elaboration, are likely to result in the formation of more precise perceptual descriptions (Norman & Bobrow, 1979) and hence, more distinctive records in memory. Another hypothesis, known as the "impoverished relational encoding" account (Arndt & Reder, 2003; Hege & Dodson, 2004; Hockley & Cristi, 1996), postulates that distinctive processing diminishes semantic activation of new but related items presented at retrieval (i.e., lures) by decreasing their associative strength to list items (Roediger, Watson, McDermott, & Gallo, 2001) or by reducing the thematic consistency of the lists (Brainerd & Reyna, 2002). Distinctive encoding has been shown to suffer when highly similar items are presented in close succession (cf., false memory). This is best exemplified in the Deese-Rodiger-McDermott (DRM) paradigm, in which highly related items (e.g., bed, rest, wake, and nap) are presented in succession (Deese, 1959; Roediger & Mcdermott, 1995). While memory for list items is generally quite high, so too are false alarms for words that are related to list items (e.g., sleep). The Fuzzy Trace Theory posits that this **ARTICLE HISTORY** 

Received 30 October 2015 Accepted 23 June 2016

Routledge

Taylor & Francis Group

Check for updates

#### **KEYWORDS** Distinctive encoding; gist encoding; memory; presentation format;

intermixed format

occurs due to the formation of gist traces that are created alongside verbatim traces (Brainerd & Reyna, 1990; Koutstaal, Schacter, Galluccio, & Stofer, 1999; Schacter, Verfaellie, & Pradere, 1996). Gist traces encapsulate the general meaning of the event but lack distinctive details that make the event unique and hence, reduce distinctive encoding processes. The current study sought to elucidate the mechanisms underlying distinctive and gist-based encoding in order to gain greater insight into how each supports successful encoding.

Researchers have used functional neuroimaging studies and false memory paradigms to investigate the neural correlates of distinctive vs. more general, gist level encoding (e.g., Dennis, Kim, & Cabeza, 2007; Kim & Cabeza, 2007; Koutstaal et al., 2003). For example, using a modified DRM paradigm, Kim and Cabeza (2007) found that activity in regions involved in semantic elaboration (i.e., left inferior frontal gyrus [IFG]) and conscious item processing (i.e., bilateral occipito-temporal and occipito-parietal cortices) predicted both true and false memories. However, greater activity in left posterior parahippocampal gyrus (PHG) and early visual cortex (BA 18/17) was associated with only subsequent true memories. Integrating results with the Fuzzy Trace Theory, the authors concluded that

CONTACT M. Natasha Rajah 🖾 maria.rajah@mcgill.ca 😑 Douglas Mental Health University Institute, McGill University and Douglas Institute, Room 2114, CIC Pavilion, 6875 LaSalle Blvd, Montreal, Quebec, Canada H4H 1R3

left IFG activity supports encoding of gist, while left PHG and visual cortex supports subsequent true memories through distinctive encoding of episodic details. Furthermore, Gutchess and Schacter (2012) found that as gist representation is strengthened at encoding, retrieval activation in both the hippocampus and visual processing regions (BA 17 and 37) decreases. The authors interpreted this finding as reflecting reduced retrieval of item-specific features in the presence of an increasing gist representation, and concluded that processes that occur under low gist conditions may best support successful distinct encoding.

Additionally, research has shown that, in the course of memory formation, frontally mediated cognitive control mechanisms (e.g., right IFG and superior medial prefrontal cortex [PFC]) support successful memory by inhibiting the processing of irrelevant or information (Anderson & Hanslmayr, 2014; Aron, Robbins, & Poldrack, 2004; Rajah, McIntosh, & Grady, 1999; Rizio & Dennis, 2013). Thus, it is arguable that successful encoding of items during blocked presentation would place greater demands on such cognitive control processes needed to inhibit gist representations that may interfere with item-specific successful encoding. With regard to gist processing, activation within the left temporal cortex has been linked to not only to general semantic processing, but also processing of semantic gist (for reviews, see Thompson-Schill, Kan, & Oliver, 2006; Wise & Price, 2006). For example, patients with semantic dementia (with damage to this region) are impaired at extracting and/or utilising semantic gist (Simons, Verfaellie et al., 2005). Furthermore, given the role of this region in language and semantic processing (Kable, Lease-Spellmeyer, & Chatterjee, 2002; Wise & Price, 2006), Dennis, Daselaar, and Cabeza (2007) have suggested that activation in left temporal cortex during both subsequent true and false memories may either represent the semantic processing of a specific category, or the integration of a category along with its exemplars. This in turn would support subsequent retrieval by providing individuals with a strong representation of semantic gist. Together, research supports the above-mentioned hypotheses, showing that distinctive encoding is promoted by perceptual and reconstructive processes supported by regions within the medial temporal lobe (MTL) and visual cortices, but can also be disrupted by presentation formats that promote more gist-based encoding. Nevertheless, the influence of the presentation format on the neural mechanisms supporting distinctive encoding is unclear.

Research in the domain of false memory has shown that many situational factors can affect the formation of gist vs. verbatim, or distinctive, traces. This includes the number of related items presented during encoding (Gutchess & Schacter, 2012; Robinson & Roediger, 1997), the amount of perceptual support for related list items (Arndt, 2010; Israel & Schacter, 1997; Schacter, Israel, & Racine, 1999), and the structure of the encoding list (Brainerd, Payne, Wright, & Reyna, 2003; Lampinen, Leding, Reed, & Odegard, 2006; McDermott, 1996; Toglia, Neuschatz, & Goodwin, 1999). For example, research has shown that distinctive encoding of highly similar items can be enhanced by the presentation of pictures during encoding, as opposed to the use of words alone (Israel & Schacter, 1997). Additionally, researchers have found that distinctive encoding is enhanced and false memories are reduced in the DRM paradigm when related items are presented in a random, intermixed format, compared to the typical blocked format (Brainerd et al., 2003; Lampinen et al., 2006; McDermott, 1996; Toglia et al., 1999). Given that the relatedness of the individual items is the same in both conditions, these results suggest that structure of list presentation may influence the encoding of itemspecific details and/or the accumulation of gist. Specifically, it has been argued that the blocked format allows for items to be grouped by themes, and as a result leads to both greater levels of, and more consistent cueing of, gist representations. In contrast, the intermixed format presentation of items is thought to enhance the saliency of the individual items.

Although a small handful of behavioural studies manipulated the presentation of items by a blocked and intermixed condition, the results were unable to speak to whether differences in neural processing underscored memory encoding across conditions. Differences in how stimuli are perceived and ultimately encoded can have significant bearing on developing interventions to improve memory performance in various populations (e.g., aging). By examining the neural correlates supporting memory success under both encoding conditions, the current study is able to better understand the mechanisms influencing successful encoding. To this end, the current study sought to investigate the role of presentation format on the utilisation of distinctive, item-specific encoding, and gist-based encoding. Specifically, the study utilised multivariate partial least squares (PLS) analysis to identify encoding networks that were directly associated with retrieval performance in a blocked relative to an intermixed presentation condition. This allowed us to examine the effect of presentation format on distinctive encoding processing at both the cognitive and neural levels. Similar to previous studies (Brainerd et al., 2003; Lampinen et al., 2006; McDermott, 1996; Toglia et al., 1999), the study manipulated the formation of conceptual gist by presenting highly similar items (e.g., pictures of different exemplars within a single category such as "dog" or "mittens") in either a blocked (high gist) or intermixed (low gist) format.

We hypothesise that successful encoding in the intermixed presentation format, compared to the blocked format, will require subjects to focus on or acquire more details of individual items, thus, leading to greater distinctive encoding. We also expect this condition to require subjects to use self-initiated strategic organisation processes to aid encoding, as stimuli are not organised in a semantic fashion (Rajah, Ames, & D'Esposito, 2008; Stuss, 1991). Thus, we predict that increased encoding activation in the bilateral early visual cortices (BA 18/19) and in left dorsolateral and anterior PFC regions will be associated with better performance in the intermixed condition. In contrast, we expect increased activity in lateral temporal cortices associated with increased semantic gist processing incurred in the blocked encoding condition. We further expect activity in right IFG to support subsequent memory in the blocked presentation format supporting enhanced cognitive control processes needed for inhibition processes (Aron et al., 2004) related to gist-based encoding. Therefore, we anticipate seeing a positive brain–behaviour association between IFG and temporal cortex activity during blocked encoding and during subsequent retrieval of these blocked items.

#### **Methods**

#### **Participants**

Twenty right-handed native English-speaking participants from the Penn State University community completed the experiment. All were screened for history of neurological disorders and psychiatric illness, alcoholism, drug abuse, and learning disabilities. Two participants were excluded from the analysis due to head motion in excess of 4 mm. An additional participant was also excluded for performing below chance and another for not completing the task, leaving data from 16 participants reported in all analyses (10 females; mean age = 20.94 years [SD = 1.65]). All participants provided written informed consent and received financial compensation for their participation. Penn State University's Institutional Review Board for the ethical treatment of human participants approved all experimental procedures.

#### Stimuli

Stimuli consisted of 1092 colour pictures of common objects. Images were obtained from an Internet image search. All backgrounds were removed and pictures were cropped and resized to an approximate size of 480 × 480 pixels (see Figure 1). Images were presented focally and equated for resolution. Seven hundred and twenty images were presented during encoding. These images consisted of 90 categories of stimuli, with eight exemplars per category. Six hundred and forty-two images were presented at retrieval including (a) 270 targets (three of the eight exemplars from each encoding category), (b) 270 related lures (three novel images associated with each encoding category), and (c) 102 unrelated lures (including three novel images from each of 34 unrelated categories) (for more details, see Dennis, Bowman, & Vandekar, 2012). Items selected as targets were counterbalanced between participants.

#### Procedure

Participants were asked to encode the 720 images while undergoing fMRI scanning (90 categories with eight exemplars per category). Retrieval was completed 24 hours later, also in the scanner. The current study focuses on encoding data only; fMRI analyses of the false memory retrieval data were reported in a previous publication (see Dennis et al., 2012). Encoding was incidental and participants were instructed to make subjective pleasantness ratings of objects as they were presented (e.g., "You will be asked to respond using a 4 point rating scale in which your pointer finger key is VERY UNPLEA-SANT, and the little finger key is VERY PLEASANT"). Participants completed six runs, each of which was approximately 8 minutes in length and included 45 exemplars per encoding run.

We manipulated levels of distinctiveness/gist encoding by presenting images either in a "blocked" or "intermixed" format within each run. Specifically, in blocked runs the eight exemplars of each category were presented consecutively, whereas in the "intermixed" format, exemplars from each category were randomly intermixed throughout the block. Each item was presented for 1000 ms and participants were given an additional 2000 ms to make their pleasantness rating, followed by a variable inter-stimulus interval (ISI) (range 1500-3000 ms in intervals of 5000 ms, with an average of 2000 ms). Encoding stimuli were back projected onto a screen that participants viewed through a mirror attached to the head coil. Stimulus presentation and behavioural data collection were performed using COGENT in MATLAB (Math Works). Images were displayed at a screen resolution of 1024 (H)  $\times$  768 (V) at 75 Hz. At the viewing distance of 143 cm, the display area was  $20^{\circ}$  (H)  $\times$ 16° (V).

During retrieval, all images were presented in the centre of the screen with three response options (Remember/ Know/New) displayed below each image. Participants completed six runs each approximately 8 minutes in length. Each image was displayed for 2500 ms and participants made their responses during that time (see Figure 1). In accord with typical task instructions, participants responded using a remember/know/new paradigm (Yonelinas, Otten, Shaw, & Rugg, 2005). The images – including targets, related lures, and unrelated lures - were pseudorandomly sorted, ensuring that no more than three images from any one category appeared in a row. During both encoding and retrieval, behavioural responses and reaction times (RTs) were recorded using a 4-button response box. Scanner noise was reduced with headphones and earplugs, and cushioning was used in the head coil to minimise head motion.

#### Image acquisition

Structural and functional images were acquired using a Siemens Trio 3T scanner equipped with a 12-channel head coil. Structural MRI images were acquired using the MPRAGE sequence (2300 ms TR, 3.41 ms TE, 230 mm field of view (FOV), 256<sup>2</sup> matrix, 160 axial slices, and 0.9 mm slice thickness). Functional MRI images were acquired



# Retrieval



Figure 1. Stimuli presentation – during encoding participants incidentally encoded eight separate items from a given category (e.g., Mittens) across six runs (three runs with stimuli presented in a blocked format by category; three runs with stimuli presented in an intermixed format) and were asked to make pleasantness ratings for each item. At retrieval, participants were told to identify which items were presented at encoding using the Remember-Know-New paradigm. Retrieval images included target items, related lures, and unrelated lures.

using an echo-planar imaging (EPI) sequence with interleaved acquisition (2000 ms TR, 30 ms TE, 240 mm FOV, a 64<sup>2</sup> matrix, 34 axial slices with 3.8 mm slice thickness resulting in 3.8 mm isotropic voxels). All images were obtained parallel to the AC-PC plane.

#### fMRI Analyses

Functional data were preprocessed with SPM8 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm). Time-series data were corrected for differences in slice acquisition times and realigned. Functional images were realigned and spatially normalised to a standard stereotaxic space using the Montreal Neurological Institute (MNI) T1-template. All images were spatially smoothed using an 8-mm isotropic Gaussian kernel. Images were checked for movement artefacts using a time-series diagnostic function **TSDiffAna** (Freiburg Brain Imaging) in MATLAB (MathWorks).

#### Spatio-temporal behaviour PLS

Multivariate behavioural spatio-temporal PLS (Behaviour ST-PLS; McIntosh & Lobaugh, 2004; http://www.rotmanbaycrest.on.ca:8080) was used to examine the direct association between brain activity and cognitive task performance. More specifically, we used Behaviour ST-PLS to determine how brain activity during blocked vs. intermixed encoding runs was directly correlated to subsequent retrieval accuracy. Retrieval accuracy was operationalised as the sensitivity index (i.e., d'), which was calculated for each participant for each condition using the following formula: Z (Hit Rate) – Z(False Alarm Rate), where Z is the inverse cumulative of the normal distribution. Note that only those trials tested at retrieval are included in this analysis. First, we constructed a baseline corrected deviation matrix for the fMRI data collected for each subject. The rows of this matrix refer to the experimental conditions of interest, which were two in the current study: correctly encoded stimuli presented in categorical blocks (blocked condition) and correctly encoded stimuli presented in randomised order (intermixed condition). The columns of this data matrix contain the event-related fMRI signal for each voxel, expressed as a baseline adjusted per cent change in BOLD signal, at each TR (time-point), from event onset to seven TRs/time lags after. Therefore, the temporal window of BOLD activity included in the data matrix for each voxel, during each condition, was 14 seconds (seven time lags of 2 seconds each). This allows for a long enough time window to detect the HRF, which is sluggish (Dale & Buckner, 1997).

Subjects' data matrices are then stacked together into a "group datamat". The group datamat is then cross-correlated with a similarly stacked vector containing the d' scores for each subject in each condition. Singular value decomposition (SVD) was then applied to this cross-correlation matrix, to generate latent variables (LVs), which consist of a singular value, a singular image, and a correlation profile for retrieval accuracy. The correlation profile shows how *d'* correlates with the condition-related brain activity, identified by the singular image, across subjects. The singular image consists of negative and positive brain saliences. Brain regions with positive voxel saliences are positively related to the correlation profile depicted for a given LV, and those with negative voxel saliences are negatively related to the correlation profiles. Thus the relationship between the singular image and the correlation profile is symmetrical. The singular value indicates the strength of the correlation between encoding-related activity in all brain voxels and the exogenous variables.

The statistical significance of each Behaviour ST-PLS LVs was determined by conducting 500 permutation tests on the singular values, which represented the proportion of the covariance matrix accounted for by each LV pair (McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh & Lobaugh, 2004). Permutations using sampling without subject replacement were conducted such that the condition-type order (i.e., rows of the data matrix) was rearranged for each subject. The probability that the permuted singular values exceed the observed singular values was calculated and only LVs for which this probability was p < .05 were deemed significant. To identify dominant and stable voxels within the singular image, a bootstrap analysis of standard errors was conducted with subject replacement (Efron & Tibshirani, 1986). We conducted 100 bootstrap samples, which allowed us to identify voxels that reliably contributed to the experimental effect within each LV. We considered local maxima throughout the brain to be reliable if the bootstrap ratio (BSR) for the regions was >3.5 (p < .0005), with a cluster size >10 voxels. We also examined the temporal profile of the identified activations to determine at which time lags the activated brain regions maximally differentiated a given LVs effect. Peak coordinates are only reported from time lags 3-5 (6-10 seconds post-event onset). Additionally, when a peak coordinate was found in more than one time lag, we report it only once, at the time lag where the bootstrap ratio was maximal. Peak coordinates were converted from MNI to Talairach space, and the Talairach and Tournoux atlas (Talairach & Tournoux, 1988) was used to identify the Brodmann area (BA) localisations of significant activations.

#### Post hoc condition-related activation analyses

It is important to note that Behaviour PLS identifies stable patterns of brain-behaviour *correlations* for specific condition-types. It *does not, however, inform us of how these brain regions activate across condition-types, within in each group.* In order to characterise the condition-related brain activation in regions identified in the PLS analysis, we extracted the mean, baseline adjusted, per cent signal change for a 4 mm cubic region surrounding peak activations identified by the PLS analysis. We then conducted *post hoc* one-way ANOVAs to determine if activity in these regions differed between blocked vs. intermixed encoding conditions.

#### Results

#### Behavioural

SPSS for Windows (version 22) was used to conduct the behavioural analyses. Because we had no a priori predictions, the differences between subsequent remember and know memories and to increase power in the current analysis, we collapsed across memory strength. Again, the sensitivity index d' was calculated using the following formula: Z(Hit Rate) – Z(False Alarm Rate), where Z is the inverse cumulative of the normal distribution. Behavioural data for "remember" and "know" trials across conditions are reported in Table 1. A paired sample t-test was performed to assess main effects of both retrieval accuracy (d') and RT. d' for the blocked (.89[.10]) and intermixed (.99[.11]) conditions revealed no significant values differences, t(15) = -1.563, p > .05. A 2(Accuracy)  $\times$  2(Item Type)  $\times$  2(Format) ANOVA examining RTs revealed a significant main effect of accuracy (F(1, 15) = 14.604, p = .002) such that correct (M = 2133.97, SD = 43.20) responses were significantly faster than incorrect (M = 2218.76, SD = 53.96) responses. Format (F(1, 15) = 7.498, p = .015) also showed a significant linear effect, showing that blocked (M = 2192.86, SD = 48.25) responses were significantly slower than Intermixed (M = 2159.88), SD = 47.70) responses. Finally, there was a significant linear interaction between accuracy and item type (F(1, 15) = 669.907, p)<.001). Specifically, correct responses were significantly slower for targets (M = 2836.51, SD = 64.75) compared to lures (M = 1431.43, SD = 31.20). On the other hand, incorrect responses were significantly faster for targets (M =1503.67, SD = 44.72) compared to lures (M = 2933.85, SD = 75.55). Furthermore, to examine more closely the influence of format on each trial-type (i.e., hits, misses, false alarms [FAs], correct rejections [CRs]) separately, post hoc paired sample t-test between format and item type showed significant difference only between blocked and intermixed CRs, t(15) = 2.544, p = .022, such that responses for intermixed correct rejections (M = 1404.51, SD = 29.18) were significantly faster than blocked correct rejections (*M* = 1458.35, SD = 36.33).

#### **Behavioural ST-PLS results**

The Behaviour ST-PLS identified one significant LV (LV1; p < .05; per cent cross-block covariance accounted for = 59.16%). The singular image, representing voxels with stable and significant activation at these lags, is shown in Figure 2(a). Local maxima for this LV for lags 3–5 are presented in Table 2. The correlation profile for this LV is

Table 1. Behavioural results.

	Remember (SE)		Combined (SE)	
Response rates				
Blocked hit	0.50 (0.03)	0.30 (0.02)	0.80 (0.03)	
Intermixed hit	0.47 (0.03)	0.31 (0.03)	0.78 (0.03)	
Blocked FA	0.22 (0.03)	0.30 (0.03)	0.51 (0.10)	
Intermixed FA	0.19 (0.03)	0.26 (0.03)	0.45 (0.03)	
Blocked d'	0.86 (0.12)	0.03 (0.08)	0.89 (0.10)	
Intermixed d'	0.88 (0.11)	0.17 (0.09)	0.99 (0.11)	
Response times (ms	5)			
Blocked hit	1288.22 (38.91)	1555.11 (48.29)	2843.33 (64.39)	
Intermixed hit	1298.11 (37.05)	1531.58 (47.01)	2829.69 (69.29)	
Blocked FA	1367.07 (45.42)	1576.65 (45.21)	314.27 (78.57)	
Intermixed FA	1362.98 (45.08)	1561.00 (50.02)	2923.98 (76.72)	

Note: The table reports the means and standard errors of the proportion of "Remember", "Know" responses, and combined ("Remember" and "Know" responses combined), as well as reaction times (RTs) and false alarms (FAs), accordingly.

shown in Figure 2(b), indicates that LV1 identified a pattern of encoding-related activity that was differentially correlated with subsequent memory accuracy (d') for items that were encoded during blocked vs. intermixed conditions. Specifically, greater activity in positive brain salience regions (see Figure 2(a); coloured orange/yellow)

during the blocked encoding condition was positively correlated with successful retrieval (d') for these items. However, increased activity in these same regions during the intermixed encoding condition was negatively correlated with subsequent retrieval for those items. In contrast, the PLS results indicated that activity in negative brain salience regions (see Figure 2(a); coloured in blue) during the intermixed encoding condition was positively correlated with subsequent retrieval of these items, whereas activity in these regions during the blocked encoding condition was negatively correlated with subsequent retrieval of those items. Therefore, even though we did not identify a significant behavioural difference in blocked vs. intermixed conditions, the Behavioural PLS results suggest there were differences in cognitive/brain states between the two encoding conditions, which directly correlated with subsequent memory performance.

Furthermore, we extracted mean activation for all peak activations listed in Table 2 and conducted *post hoc* one-way ANOVAs to determine which regions not only exhibited significant brain-behaviour correlations, but also exhibited significant differences in condition-related



**Figure 2.** Latent Variable 1 (LV1) – regions in which activity during blocked vs. intermixed conditions was differentially related to subsequent retrieval accuracy (d'). (a) The singular image for LV1 at bootstrap ratio threshold of ±3.5 (p < .0005), lags 3–5. The colour-bar represents the strength of positive and negative bootstrap salience values. Regions coloured in orange/yellow (positive brain salience regions) are areas in which encoding activity during blocked conditions was positively correlated with subsequent retrieval for block-encoded items; but in which encoding activity during intermixed conditions was negatively correlated with subsequent retrieval for intermixed-encoded items. Regions coloured in blue (negative brain salience regions) reflect the inverse brain–behaviour correlation effects for blocked and intermixed conditions. (b) The correlation profile for this LV, indicating that LV1 identified a pattern of encoding-related activity that was differentially correlated with subsequent memory accuracy (d') for items that were encoded during blocked vs. intermixed conditions.

#### 692 🔄 I. C. TURNEY ET AL.

Talairach coordinates										
Temporal lag	Bootstrap ratio	Spatial extent	x	у	Z	HEM	Gyral location	Brodmann area		
Positive salience	es (yellow): Regions in	which increased activ	vity positive	ly correlate	d with subs	equent retri	eval (d') for blocked condition t	rials, but negatively		
correlated wit	h subsequent retrieva	I for the intermixed	trials.							
3	5.53	17	-57	-31	51	Left	Postcentral gyrus	BA 2*		
3	4.63	16	44	14	20	Right	Inferior frontal gyrus	BA 45*		
4	4.73	11	-12	-7	54	Left	Medial frontal gyrus	BA 6		
Negative salienc	es (blue): Regions in w	hich increased activit	y positively	correlated	with subsec	quent retriev	al (d') for intermixed condition t	rials, but negatively		
correlated wit	h subsequent retrieva	I for the blocked tria	ls.							
3,4	-10.19	84	-47	-16	39	Left	Precentral gyrus	BA 4		
3,4	-5.76	83	-15	3	-2	Left	Lentiform nucleus	LGP*		
3	-5.39	54	-29	-37	44	Left	Postcentral gyrus	BA 3		
3	-5.05	13	-12	-99	-12	Left	Lingual gyrus	BA 17*		
3,4,5	-7.75	46	-9	-26	73	Left	Medial frontal gyrus	BA 6		
3	-4.53	11	-32	-16	2	Left	Lentiform nucleus	Putamen		
3,4	-7.96	49	48	43	16	Right	Middle frontal gyrus	BA 46		
3,4,5	-7.71	81	37	-27	43	Right	Postcentral gyrus	BA 2		
3,4,5	-8.31	41	23	45	33	Right	Superior frontal gyrus	BA 9*		
3.4	-5.81	38	23	-28	56	Right	Postcentral gyrus	BA 3		
3	-5.53	19	54	20	31	Right	Middle frontal gyrus	BA 9		
3.4	-5.51	17	23	-86	-3	Right	Middle occipital gyrus	BA 18		
3	-5.26	13	13	0	25	Right	Caudate	Caudate Body		
3	-5.08	20	48	-15	-3	Right	Superior temporal gyrus	BA 22		
3	-4.90	12	2	41	32	Right	Medial grontal gyrus	BA 9		
3,4,5	-5.51	30	41	-26	-4	Right	Insula	BA 13		
3,4,5	-7.30	91	26	-66	49	Right	Superior parietal lobule	BA 7		
4	-9.23	84	-2	-39	65	Left	Paracentral lobule	BA 5		
4,5	-5.47	12	-23	-70	51	Left	Precuneus	BA 7		
4	-5.15	13	-47	-58	35	Left	Inferior parietal lobule	BA 40		
4	-4.61	12	-53	20	32	Left	Middle frontal gyrus	BA 9*		
4	-8.81	11	34	7	-18	Riaht	Superior temporal gyrus	BA 38		
4	-6.79	21	48	-47	-10	Right	Occipito-temporal	BA 37		
4	-6.11	56	40	-44	41	Right	Inferior parietal lobule	BA 40		
4	-5.71	19	19	7	63	Right	Superior frontal gyrus	BA 6		
4.5	-6.15	15	9	20	37	Right	Cinculate gyrus	BA 32		
5	-7.12	31	-35	22	-18	left	Inferior frontal gyrus	BA 47		
5	-6.45	54	-5	13	29	Left	Cinculate gyrus	BA 24		
5	-6.22	15	19	-28	56	Right	Precentral gyrus	BA 4		
5	-5.85	12	9		25	Right	Cinquilate gyrus	BA 24		
5	-5.72	17	5	_19	36	Right	Cingulate gyrus	BA 24		
5	-5.28	10	33	15	44	Right	Middle frontal gyrus	BA 6*		

Table 2. Local maxima for LV1: blocked vs. intermixed condition difference.

Note: Temporal lag represents the time after event onset, when a cluster of voxels exhibited a contrast effect of interest. The bootstrap ratio threshold was set to  $\pm$  3.5 and identified dominant and stable activation clusters. The spatial extent refers to the total number of voxels included in the voxel cluster (threshold = 10). The stereotaxic coordinates are measured in millimetres, and gyral location and Brodmann areas (BAs) were determined by referring to Talairach and Tournoux (1988). HEM = cerebral hemisphere in which the activation occurred. Regions marked with \* were regions that exhibited significant differences in task-related activity.

activation. Regions that exhibited significant differences in condition-related activity are marked with an asterisk (\*) in Table 2. We plotted the baseline corrected mean per cent signal change during blocked encoding and intermixed encoding conditions for PFC and visual regions from LV 1 that also exhibited significant condition-related differences in activity in Figure 3. This graph indicates that all regions identified exhibited more activity during blocked > intermixed encoding.

#### Discussion

The primary goal of the current study was to examine the effect of presentation format on distinctive encoding processing from both a cognitive and neural perspective. We predicted that presentation format would be related to task performance (i.e., RT and d'). Contrary to our predictions, we found no significant difference in either retrieval

accuracy (d') or RT between the blocked and intermixed format (d': t(15) = -1.563, p > .05; RT: t(15) = .463, p > .05).Additionally, we investigated response time differences between conditions. The only significant difference to emerge was a difference in RT between intermixed CRs and blocked CRs such that intermixed CRs were significantly faster than blocked CRs. The fact that it took subjects a longer time to reject lures during blocked vs. intermixed conditions is consistent with our hypothesis of greater gist processing, and reduced distinctive encoding in the blocked condition. While the lack of differences in accuracy or RT performance between hits across conditions was contrary to our predictions, a recent meta-analytic review suggests that distinctive encoding does not always serve to reduce false memories in DRM paradigms (Huff, Bodner, & Fawcett, 2015). This meta-analytic review suggested that alternating condition-type, as done in our study (where encoding condition alternated across runs),



Figure 3. Latent Variable 1 (LV1) – bar graphs of mean per cent signal change, relative to baseline, in LV1 regions that exhibited significant differences in taskrelated activation. Thus, the following regions showed both significant brain–behaviour correlation patterns (as identified by PLS) and significant differences in brain activity between blocked vs. intermixed conditions: right Inferior frontal gyrus (BA 45), left lingual gyrus (BA 17), right superior frontal gyrus (BA 9), left middle frontal gyrus (BA 9) and right middle frontal gyrus (BA 6). Regions are identified by hemisphere and Brodmann area.

may reduce the effectiveness of the distinctive encoding task. The review suggests that a stricter blocked design (i.e., first three runs of all distinctive ["blocked"] followed by three runs of all non-distinctive items ["intermixed"]) may be necessary to induce behavioural differences. Future studies should examine the effectiveness of using this stricter segregated design.

Although the overall behavioural findings were surprising, the current results afforded us the ability to directly examine how successful encoding during blocked vs. intermixed conditions correlated with brain activity in the absence of behavioural confounds, that is, task difficulty effects between conditions. Thus, allowing us to examine task differences in cognitive/brain state that directly correlated with encoding success. Using multivariate PLS analysis, we identified a pattern of whole brain activity that was differentially correlated to subsequent memory effects for stimuli encoded during the blocked vs. intermixed conditions. Specifically, this analysis yielded three key findings: (1) Even though there were no behavioural differences in retrieval accuracy for blocked vs. intermixed conditions, there were distinct differences in brain-behaviour correlations between conditions, highlighting that different cognitive processes subserving performance on these tasks (see Figure 2(a)). (2) Encoding activity, in a distributed set of brain regions, including bilateral occipital cortex, middle frontal gyrus (MFG) and right superior frontal gyrus (SFG) was positively correlated with subsequent retrieval during the intermixed condition. Surprisingly, the post hoc activation analyses indicated there was decreased activity in these same regions during intermixed encoding, relative to baseline. (3) Encoding activity in right IFG during blocked encoding was directly correlated with better subsequent memory for block-encoded items. In addition, post hoc analysis indicated there was greater activity in this region during blocked vs. intermixed conditions (see Figure 3). These results are discussed in depth below.

## Activation supporting subsequent memory for intermixed-encoded items

We hypothesised that presenting encoding items in an intermixed format would encourage more distinctive encoding processing, as it promotes attention to the individual identity of each presented object and it prohibits the build-up of categorical gist across related items presented in succession that is typical in most DRM paradigms (also present in the current blocked condition). As such, we posited that such distinctive encoding would be more reliant on frontally mediated cognitive control process, for selecting an appropriate encoding strategy given that no overt strategy (i.e., semantic relatedness) is provided. This hypothesis was based on previous word-list learning paradigms comparing performance of frontal lobe patients vs. healthy controls, which have shown that damage to the frontal cortex, particularly the dorsolateral PFC, impedes memory performance on intermixed, but not semantically blocked word stimuli (Levine et al., 1998; Stuss, Craik, Sayer, Franchi, & Alexander, 1996). Consistent with this prediction, we observed that greater PFC activity during intermixed encoding was positively correlated with subsequent retrieval, which may reflect the greater strategic organisation demands for this condition.

We also hypothesised that distinctive encoding during the intermixed condition would permit subjects to focus their encoding on item-specific perceptual details. That is, we predicted that the intermixed presentation would allow participants to focus on item-specific details, as item features and identity varied on a trial-by-trial basis. Previous studies have attributed detailed visual encoding to increased activity within the visual cortex and fusiform gyrus (Dennis et al., 2012; Dennis, Johnson, & Peterson, 2014; Marche, Brainerd, & Reyna, 2010; Moritz, Glascher, Sommer, Buchel, & Braus, 2006; Slotnick & Schacter, 2004, 2006). Thus the positive correlation between neural activity in the occipital-fusiform regions during intermixed encoding and subsequent retrieval for intermixed-encoded items is consistent with our hypothesis and with prior findings examining distinctive encoding processes.

Interestingly, our post hoc activation results indicated that although activity in a variety of brain regions during intermixed encoding was positively correlated with subsequent retrieval, few of these regions exhibited activation differences between blocked vs. intermixed conditions. Specifically, we observed decreased activity in left lingual, right superior frontal, and bilateral middle frontal gyri during intermixed encoding, relative to baseline. This suggests that despite being correlated with performance in the intermixed condition, overall activity was greater in the blocked condition in the foregoing regions. While initially perplexing to reconcile, taken together, results suggest that although activity may be greater in regions such as the MFG and visual cortex, when items are presented within blocked categories, this increase in activity does not support subsequent memory behaviour. The results highlight the need to consider behaviour as well as activation metrics in neuroimaging analyses.

We predicted that categorical processing and semantic gist mediated by the left lateral temporal cortex would contribute to successful memory in the blocked condition. Contrary to this prediction, the B-PLS results indicated that there was a positive correlation between encoding activity in right superior temporal gyrus (STG) and subsequent retrieval for intermixed items, and a negative correlation between encoding activity in STG and subsequent retrieval for blocked items. However, the post hoc activation analysis did not identify a significant difference in right STG activity between the two encoding conditions. In other words, there was a significant difference in brain-behaviour correlation between conditions, in presence of no significant difference in condition-related activation. That is, activity in STG, a region shown to support semantic labelling and semantic gist processing (Noppeney et al., 2007; Price, 2000; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Wise & Price, 2006), was negatively correlated with subsequent memory in the blocked condition. One explanation for the current finding is that, given that the semantic label never changed across blocked trials, semantic gist and semantic labelling across all blocked trials may have been unnecessary and in fact, detrimental to successful performance in the blocked condition. That is, successful memory in the blocked condition needed to overcome this processing as the same semantic label was applicable to all items in a given block (Brainerd & Reyna, 1990; Schacter et al., 1996) and thus did not help distinguish them for later memory.

## Activation supporting subsequent memory for block-encoded items

As noted above, while we anticipated that the blocked encoding format would elicit greater processing in regions supporting semantic gist and semantic labelling (i.e., left lateral temporal cortex and left IFG), the results did not support our predictions. We also predicted that successful encoding of items presented during the blocked condition would place greater demands on cognitive control processes necessary for inhibiting the formation of inter-stimulus associations and gist-based processing. To this end, we did observe a significant positive correlation between activity in right IFG and subsequent retrieval of blocked items. Moreover, activity in right IFG was greater during blocked than the intermixed encoding condition. Thus, evidence suggests that right IFG activity durina blocked > intermixed condition may reflect greater demands on top-down inhibitory processing (Aron et al., 2004; Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010; Rajah and D'Esposito, 2005) necessary to resolve semantic inference between blocked items.

Interestingly, studies that have examined fMRI activity during false vs. true recognition, have observed greater IFG activity during false recognition for items encoded under conditions emphasising conceptual, rather than perceptual, gist (Garoff-Eaton, Kensinger, & Schacter, 2007; Gutchess & Schacter, 2012). Taken together, these findings suggest that although encoding-related activity in right IFG supports subsequent retrieval, retrieval-related activity in this region may not be beneficial. This contrast, particularly the role of IFG contributions to memory success during a false memory paradigm, warrants further attention. Future studies should aim to directly examine how IFG activity at encoding vs. retrieval correlate with memory performance for block-encoded items.

### **Limitations and future directions**

The current study was able to identify different patterns of brain activity during blocked vs. intermixed presented encoding, which were directly predictive of subsequent retrieval. As a result, we were able to better understand the role of various brain regions that support memory formation within each encoding condition. Nevertheless, there were some limitations to consider. One limitation that may have influenced results may be due to the partial variance explained by the encoding trials that were not tested at retrieval. Particularly, out of the eight exemplars per category from encoding, only three were tested at retrieval while the other five exemplars were not included in the retrieval test and thus necessitating that they be treated as trial types of no interest in the subsequent memory analysis. These exemplars were included for the sole purpose of building gist and were not included at retrieval because we did not want to overwhelm participants at retrieval. Thus, only a subset of encoding trials was included at test. Future studies could adjust for this by including all encoding trials in a subsequent memory test. Utilising this and/or other enhanced designs (as mentioned above) to examine ways to increase distinctive encoding in older adults may prove particularly beneficial,

especially due to the well-known age-related increases in false memories. Consequently, this may provide an even clearer understanding of the neural and cognitive processes underlying distinctive encoding.

Secondly, as noted above, possibly due to our study design, our task manipulation did not elicit any behavioural differences between presentation conditions. Despite this, our Behaviour PLS approach allowed us to identify different brain-behaviour associations across conditions, showing that behavioural performance between conditions was reliably associated with differentiated patterns of neural activity. Nevertheless, future work should further examine this phenomenon, considering flaws in our abovementioned task design.

### Conclusions

The current study aimed to examine the influence of presentation format on subsequent memory performance and neural activity supporting successful encoding. Our study demonstrated that the sequence in which information is presented during encoding affected the degree to which distinctive encoding was engaged. Specifically, as predicted, we observed that by interleaving items across categories, the intermixed presentation condition lead to more distinctive or item-specific encoding. We observed this neurally by showing activity that was positively correlated with task performance, in regions associated with strategy use and visual processing (e.g., frontal and visual cortices, respectively). On the other hand, as predicted, we observed that by presenting similar items in a blocked format, the blocked presentation condition supported successful subsequent memory, but would require more inhibitory and gist-based processing. We observed this neurally by showing activity that positively correlated with task performance, in regions linked to these processes (e.g., right IFG).

Together, our results can be related to those found in false memory studies, where true memories are supported by greater attention and processing of item-specific details, while false memories are supported by more semantic processing, being more reliant on gist-based memories. Furthermore, these findings extend our understanding of the Fuzzy Trace Theory, as well as the neural mechanisms underlying the role of presentation format on encoding processes. Overall, results show that successful memory can, in fact, occur under both presentation conditions. However, it is evident that different cognitive and neural processes underlie encoding in each encoding format.

#### Acknowledgements

The authors wish to thank Christina E. Webb for help with initial data analyses and the Penn State Social, Life, & Engineering Sciences Imaging Center (SLEIC) 3T MRI Facility.

#### **Disclosure statement**

No potential conflict of interest was reported by the authors.

#### Funding

This work was supported by a National Science Foundation grant [BCS1025709] awarded to NAD and was conducted while NAD was an AFAR Research Grant recipient from the American Federation for Aging Research, as well as a Graduate Research Fellowship from the National Science Foundation awarded to ICT [DGE1255832], a Fonds de Recherche Santé Québec postdoctoral training award to DM, and a CIHR Operating Grant [MOP126105] and FRQ-S Junior 2 Award to MNR.

#### References

- Anderson, M. C., & Hanslmayr, S. (2014). Neural mechanisms of motivated forgetting. *Trends in Cognitive Sciences*, 18(6), 279–292. doi:10. 1016/j.tics.2014.03.002
- Arndt, J. (2010). The role of memory activation in creating false memories of encoding context. *Journal of Experimental Psychology*. *Learning Memory, and Cognition*, 36(1), 66–79. doi:10.1037/a0017394
- Arndt, J., & Reder, L. M. (2003). The effect of distinctive visual information on false recognition. *Journal of Memory and Language*, 48(1), 1–15.
- Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, 6, 115–116.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, 8(4), 170– 177.
- Brainerd, C. J., Payne, D. G., Wright, R., & Reyna, V. F. (2003). Phantom recall. *Journal of Memory and Language*, 48(3), 445–467. doi:10. 1016/S0749-596x(02)00501-6
- Brainerd, C. J., & Reyna, V. F. (1990). Gist is the gist: The fuzzy-trace theory and new intuitionism. *Developmental Review*, 10, 3–47.
- Brainerd, C. J., & Reyna, V. F. (2002). Fuzzy-trace theory and false memory. Current Directions in Psychological Science, 11, 164–169.
- Dale, A. M., & Buckner, R. L. (1997). Selective averaging of rapidly presented individual trials using fMRI. *Human Brain Mapping*, 5 (5), 329–340.
- Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology*, 58(1), 17–22.
- Dennis, N. A., Bowman, C. R., & Vandekar, S. N. (2012). True and phantom recollection: An fMRI investigation of similar and distinct neural correlates and connectivity. *Neuroimage*, 59(3), 2982–2993. doi:10.1016/j.neuroimage.2011.09.079
- Dennis, N. A., Daselaar, S., & Cabeza, R. (2007). Effects of aging on transient and sustained successful memory encoding activity. *Neurobiology of Aging*, 28(11), 1749–1758. doi:S0197-4580(06) 00239-9 [pii] 10.1016/j.neurobiolaging.2006.07.006
- Dennis, N. A., Johnson, C. E., & Peterson, K. M. (2014). Neural correlates underlying true and false associative memories. *Brain and Cognition*, 88, 65–72.
- Dennis, N. A., Kim, H. K., & Cabeza, R. (2007). Effects of aging on the neural correlates of true and false memory formation. *Neuropsychologia*, 45, 3157–3166.
- Efron, B., & Tibshirani, R. (1986). Bootstap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science*, 1(1), 54–75.
- Garoff-Eaton, R. J., Kensinger, E. A., & Schacter, D. L. (2007). The neural correlates of conceptual and perceptual false recognition. *Learning* and Memory, 14(10), 684–692.
- Gutchess, A. H., & Schacter, D. L. (2012). The neural correlates of gistbased true and false recognition. *Neuroimage*, 59(4), 3418–3426. doi:10.1016/j.neuroimage.2011.11.078
- Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *Neuroimage*, *50*, 1313–1319.

- Hege, A. C., & Dodson, C. S. (2004). Why distinctive information reduces false memories: evidence for both impoverished relational-encoding and distinctiveness heuristic accounts. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 30(4), 787–795.
- Hockley, W. E., & Cristi, C. (1996). Tests of encoding tradeoffs between item and associative information. *Memory and Cognition*, 24(2), 202–216.
- Huff, M. J., Bodner, G. E., & Fawcett, J. M. (2015). Effects of distinctive encoding on correct and false memory: a meta-analytic review of costs and benefits and their origins in the DRM paradigm. *Psychonomic Bulletin and Review*, 22(2), 349–365. doi:10.3758/ s13423-014-0648-8
- Israel, L., & Schacter, D. L. (1997). Pictorial encoding reduces false recognition of semantic associates. *Psychonomic Bulletin and Review*, 4(4), 577–581. doi:10.3758/Bf03214352
- Jacoby, L. L., Craik, F. I. M., & Begg, I. (1979). Effects of decision difficulty on recognition and recall. *Journal of Verbal Learning and Verbal Behavior*, 18(5), 585–600.
- Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002). Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience*, 14(5), 795–805.
- Kim, H. K., & Cabeza, R. (2007). Differential contributions of prefrontal, medial temporal, and sensory-perceptual regions to true and false memory formation. *Cerebral Cortex*, *17*, 2143–2150.
- Koutstaal, W., Reddy, C., Jackson, E. M., Prince, S., Cendan, D. L., & Schacter, D. L. (2003). False recognition of abstract versus common objects in older and younger adults: testing the semantic categorization account. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 29*(4), 499–510.
- Koutstaal, W., Schacter, D. L., Galluccio, L., & Stofer, K. A. (1999). Reducing gist-based false recognition in older adults: encoding and retrieval manipulations. *Psychology of Aging*, 14(2), 220–237.
- Lampinen, J. M., Leding, J. K., Reed, K. B., & Odegard, T. N. (2006). Global gist extraction in children and adults. *Memory*, 14(8), 952–964. doi:10.1080/09658210601008957
- Levine, B., Stuss, D. T., Milberg, W. P., Alexander, M. P., Schwartz, M., & Macdonald, R. (1998). The effects of focal and diffuse brain damage on strategy application: evidence from focal lesions, traumatic brain injury and normal aging. *Journal of the International Neuropsychological Society*, 4(3), 247–264.
- Marche, T. A., Brainerd, C. J., & Reyna, V. F. (2010). Distinguishing true from false memories in forensic contexts: Can phenomenology tell us what is real. *Applied Cognitive Psychology*, 24(8), 1168–1182.
- McDermott, K. B. (1996). The persistence of false memories in list recall. Journal of Memory and Language, 35(2), 212–230. doi:10.1006/jmla. 1996.0012
- McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial pattern analysis of functional brain images using partial least squares. *Neuroimage*, 3(3), 143–157. doi:10.1006/nimg.1996.0016
- McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: Applications and advances. *Neuroimage*, 23, S250–S263. doi:10.1016/j.neuroimage.2004.07.020
- Moritz, S., Glascher, J., Sommer, T., Buchel, C., & Braus, D. F. (2006). Neural correlates of memory confidence. *Neuroimage*, *33*(4), 1188–1193.
- Noppeney, U., Patterson, K., Tyler, L. K., Moss, H., Stamatakis, E. A., Bright, P., ... Price, C. J. (2007). Temporal lobe lesions and semantic impairment: A comparison of herpes simplex virus encephalitis and semantic dementia. *Brain*, 130(Pt 4), 1138–1147.
- Norman, D. A., & Bobrow, D. G. (1979). Descriptions Intermediate stage in memory retrieval. *Cognitive Psychology*, 11(1), 107–123.
- Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, 197(Pt 3), 335–359.

- Rajah, M. N., & D'Esposito, M. (2005). Region-specific changes in prefrontal function with age: A review of PET and fMRI studies on working and episodic memory, *Brain*, 128, 1964–1983.
- Rajah, M. N., Ames, B., & D'Esposito, M. (2008). Prefrontal contributions to domain-general executive control processes during temporal context retrieval. *Neuropsychologia*, 46(4), 1088–1103. doi:10.1016/ j.neuropsychologia.2007.10.023
- Rajah, M. N., McIntosh, A. R., & Grady, C. L. (1999). Frontotemporal interactions in face encoding and recognition. *Cognitive Brain Research*, 8(3), 259–269.
- Rizio, A. A., & Dennis, N. A. (2013). The neural correlates of cognitive control: Successful remembering and intentional forgetting. *Journal of Cognitive Neuroscience*, 25(2), 297–312. doi:10.1162/ jocn\_a\_00310
- Robinson, K. J., & Roediger, H. L. (1997). Associative processes in false recall and false recognition. *Psychological Science*, 8, 231–237.
- Roediger, H. L., & Mcdermott, K. B. (1995). Creating false memories Remembering words not presented in lists. *Journal of Experimental Psychology-Learning Memory and Cognition*, 21(4), 803–814.
- Roediger, H. L., Watson, J. M., McDermott, K. B., & Gallo, D. A. (2001). Factors that determine false recall: A multiple regression analysis. *Psychonomic Bulletin and Review*, 8(3), 385–407.
- Schacter, D. L., Israel, L., & Racine, C. (1999). Suppressing false recognition in younger and older adults: The distinctiveness heuristic. *Journal of Memory and Language*, 40(1), 1–24. doi:10.1006/jmla. 1998.2611
- Schacter, D. L., Verfaellie, M., & Pradere, D. (1996). The neuropsychology of memory illusions: False recall and recognition in amnesic patients. *Journal of Memory and Language*, 35, 319–334.
- Simons, J. S., Gilbert, S. J., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. *Journal of Neurophysiology*, 94 (1), 813–820.
- Simons, J. S., Verfaellie, M., Hodges, J. R., Lee, A. C., Graham, K. S., Koutstaal, W., ... Budson, A. E. (2005). Failing to get the gist: Reduced false recognition of semantic associates in semantic dementia. *Neuropsychology*, 19(3), 353–361.
- Slotnick, S. D., & Schacter, D. L. (2004). A sensory signature that distinguishes true from false memories. *Nature Neuroscience*, 7(6), 664–672.
- Slotnick, S. D., & Schacter, D. L. (2006). The nature of memory related activity in early visual areas. *Neuropsychologia*, 44(14), 2874–2886.
- Stuss, D. T. (1991). Self, awareness, and the frontal lobes: A neuropsychological perspective. In J. Strauss & G. R. Goethals (Eds.), *The self: Interdisciplinary approaches* (pp. 255–278). New York, NY: Springer-Verlag.
- Stuss, D. T., Craik, F. I. M., Sayer, L., Franchi, D., & Alexander, M. P. (1996). Comparison of older people and patients with frontal lesions: Evidence from word list learning. *Psychology and Aging*, *11*(3), 387–395. doi:10.1037/0882-7974.11.3.387
- Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain. Stuttgart: Thieme.
- Thompson-Schill, S. L., Kan, I. P., & Oliver, R. T. (2006). Functional neuroimaging of semantic memory. In R. Cabeza & A. Kingstone (Eds.), Handbook of functional neuroimaging of cognition (pp. 149–190). Cambridge, MA: MIT Press.
- Toglia, M. P., Neuschatz, J. S., & Goodwin, K. A. (1999). Recall accuracy and illusory memories: When more is less. *Memory*, 7(2), 233–256. doi:0.1080/741944069
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *Journal of Neuroscience*, 25(11), 3002–3008.
- Wise, R. J. S., & Price, C. J. (2006). Functional imaging of language. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging* of cognition (2nd ed, pp. 191–228). Cambridge, MA: MIT Press.